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The iterated continuous prisoner's dilemma game cannot explain the evolution of interspecific mutualism in unstructured populations

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Abstract

The evolutionionary origin of inter- and intra-specific cooperation among non-related individuals has been a great challenge for biologists for decades. Recently, the continuous prisoner's dilemma game has been introduced to study this problem. In function of previous payoffs, individuals can change their cooperative investment iteratively in this model system. Killingback and Doebeli (Am. Nat. 160 (2002) 421–438) have shown analytically that intra-specific cooperation can emerge in this model system from originally non-cooperating individuals living in a non-structured population. However, it is also known from an earlier numerical work that inter-specific cooperation (mutualism) cannot evolve in a very similar model. The only difference here is that cooperation occurs among individuals of different species. Based on the model framework used by Killingback and Doebeli (2002), this Note proves analytically that mutualism indeed cannot emerge in this model system. Since numerical results have revealed that mutualism can evolve in this model system if individuals interact in a spatially structured manner, our work emphasizes indirectly the role of spatial structure of populations in the origin of mutualism.

Keywords: Adaptive dynamics; Coevolution; Evolutionary stability; Reciprocal altruism; Variable investment

Mutualistic interactions between members of different species are widespread and play a central role in ecosystems (Boucher et al., 1982; Bronstein, 2001a, b). However, the evolution of mutualism has been a great challenge for theoreticians for decades. How can mutualist individuals emerge in populations where all the others are non-mutualists, and how can mutualists prevent cheaters from spreading in the population?

The classical theoretical framework for studying cooperation of unrelated individuals *within a species* is the Prisoner's Dilemma Game (Trivers, 1971), in which partners can choose either a defective (cheating) or a cooperative strategy. If both partners defect, they get a smaller fitness than if both cooperate, but a defector has an even higher fitness value if its opponent cooperates. However, the cheated cooperator receives the smallest fitness if its opponent is a defector. It is easy to see that defection is the only evolutionary stable state in this model, and cooperators cannot spread in a defecting population. On the other hand, defectors can invade and destroy cooperation in a cooperative population (Trivers, 1971; Axelrod and Hamilton, 1981). Cooperative strategies emerge and are stable against the invasion of defective ones if individuals can interact with each others repeatedly (Axelrod and Hamilton, 1981; Nowak and Sigmund, 1992, 1993). The general conclusions of intensive work in this field are that the successful strategies are either those that punish defector and reward cooperation in repeated encounters (Tit-for-Tat, Generous Tit-for-Tat) or those that retain their previous successful strategy (Pavlov).

Doebeli and Knowlton (1998) realized that there is no way for individuals to vary the degree of cooperation in

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these model systems, which is an unrealistic assumption in many biological situations. Therefore, they introduced an *interspecific* prisoner's dilemma game where the payoffs can change according to the investments made by the partners. The level of investment I_h by a host individual involves a cost $C(I_h)$ to the host and gives a benefit $B(I_h)$ to its symbiont partner. (Naturally, if the investment is zero then the cost and the benefit are zero too.) Thus if the symbiont partner invests I_s then the payoff for the host is $S(I_h, I_s) = B(I_s) - C(I_h)$ and similarly, the payoff of the symbiont is $S(I_s, I_h) = B(I_h) - C(I_s)$. (Species are called "host" and "symbiont" only for convenience, but they have a completely symmetrical role in the mutualistic interaction.) In the special case when one of them makes no investment to the interaction we retrieve the classical prisoner's dilemma game again (Table 1).

Mutualistic connections were considered by Doebeli and Knowlton (1998) as a series of prisoner's dilemma games with variable investment, where the investment of a partner depends on its payoff received in the previous round. Interaction is a general phrase covering different kinds of exchange of commodities (Bronstein, 2001a, b). The investment decision is determined by two parameters: α, the initial offer, and β, the reward rate or the rate of increase of investment depending on the payoff S in the preceding round. So the investment of a host in round $k+1$ is

$$I_h^{(k+1)} = \alpha_h + \beta_h S(I_h^{(k)}, I_s^{(k)}), \tag{1}$$

where $S(I_h^{(k)}, I_s^{(k)})$ is the payoff of the host individual in round k, if it invested $I_h^{(k)}$ and its symbiont opponent invested $I_s^{(k)}$ in the previous interaction. To avoid negative investment $I_h^{(k+1)}$ is set to zero if $S(I_h^{(k)}, I_s^{(k)}) < -\alpha_h/\beta_h$. Similarly, the opponent's investment in the $k+1$-th round is

$$I_s^{(k+1)} = \alpha_s + \beta_s S(I_s^{(k)}, I_h^{(k)}), \tag{2}$$

where α_s and β_s are initial offer and reward rate of the opponent. Since benefit generally increases less at higher investment (see e.g. Altmann, 1979; Schulman and Rubenstein, 1983), Doebeli and Knowlton (1998) used a concave function for $B(I)$, namely $B(I) = B_0[1 - exp(-B_1 I)]$. They assumed that cost increases linearly, that is $C(I) = C_0 I$. The parameters B_0, B_1 and C_0 are positive constants describing the cost–benefit relations for all individuals. It is worth investing in the interaction only if $B_0 > C_0$, and therefore this relation is assumed in the following. There are a fixed number of mutualistic interactions between two generations, and the fitness of an individual is the sum of payoffs collected in each round.

Table 1
Payoff matrix when the cooperative (C) strategy invests $I > 0$ and the defective (D) does not invest into the interaction

	C	D
C	$R = B(I) - C(I)$	$S = -C(I)$
D	$T = B(I)$	$P = 0$

The matrix describes the classical prisoner's dilemma game if $T > R > P > S$ and $2R > (T + S)$, which is valid if $B(I) > C(I)$.

The partners, independent of which species they belong to, have an initial phenotype (α, β), so initially all of them have the same fitness. However, slightly different mutant phenotypes can emerge by chance in both populations in every generation. If a mutant has a higher fitness than the resident type, the latter is replaced by the mutant phenotype. Invasion is thus assumed to imply fixation (Doebeli and Knowlton, 1998). Mutualism emerges if the originally very small, but positive α and β phenotypic traits evolve towards higher positive values.

However, according to numerical simulations mutualism cannot evolve if the partners live in "well-mixed" populations without spatial structure (Doebeli and Knowlton, 1998). Well-mixedness means that the probability of interactions between different phenotypes is equal to the product of their relative frequencies, and is assumed here for both intraspecific competition and interspecific mutualism. This assumption makes the model more tractable, but neglects the spatial structure present in most populations. It has been known for some time that spatially structured evolutionary games behave differently and in a more complex manner than "well-mixed" models (Nowak and May, 1992). It is thus not surprising that Doebeli and Knowlton (1998) placed the individuals of interacting species on the grid points of separate lattices. An individual in the first population can interact with the individual on the same grid point of the other lattice. The fitness of each individual is given by the sum of payoffs received in the *interspecific* interactions, which determines the competitive success with their local neighbors *within* the species. The phenotype which has the highest fitness among the neighbors (including the focal individual itself) will enter the next generation at the chosen site. It has been shown numerically that mutualism can emerge in this spatially explicit system, particularly if dispersion is absent or limited, and some stochasticity is present in the competition or selection processes (Doebeli and Knowlton, 1998). One of the crucial difference between the "well-mixed" and lattice models that the successful strategies spread by growing patches in the latter case. Thus the similar (or identical) strategies interact with each other with a high probability in the spatially structured models, while to meet a similar (e.g. cooperative) strategy depends on their relative frequencies in the well-mixed systems. This "viscosity" of spatial models enhance the benefit of cooperative strategies in a similar way as kin-selection acts on the evolution of cooperation in well-mixed models (van Baalen and Rand, 1998).

Variable investment is also a fruitful concept in studying cooperation among non-related individuals that belong to the same species. The model of this problem is very similar to that introduced above, but now the partners are members of the same population. Killingback et al. (1999) considered a population where individuals live on a two-dimensional lattice and play a non-iterated prisoner's dilemma game with variable investment. Partners interact with their eight nearest neighbors. The fitness of each individual is given by the sum of payoffs received in the interactions with all neighbors. Similar to the two species case, the phenotype which has the highest fitness among the neighbors will enter the next generation. If phenotypes are allowed to change their investment by mutations, the population evolves to cooperation in this spatially structured model despite there being no iteration of investment (Killingback et al., 1999). Furthermore, cooperation emerges and is stable against the invasion of defectors even in a well-mixed population (Killingback and Doebeli, 2002) assuming that investment can change according to the iteration process described above. The latter was confirmed by analytical results. Killingback and Doebeli (2002) have shown that if the initial reward rate β exceeds a critical level $\beta_c = C'(0)/[B'(0)^2 - C'(0)^2]$ where $C'(0), B'(0)$ means the derivative of cost and benefit at zero investment, then both α and β evolve towards higher positive values. Evolution thus leads to cooperation in all cases, independently of the initial offer if the initial reward rate is high enough. The higher the benefit is compared to the cost at low investment, the lower the threshold β_c which must be exceeded. However, as we have stressed above, simulations suggest that there is no way for interspecific mutualism in a well-mixed population to evolve, even if iterated investment is built into the model. What is the difference between within species cooperation and interspecific mutualism, that can lead to such different behavior? The differences are intuitively clear: individuals compete with the con-specifics and cooperate with the inter-specifics in the mutualistic case, while cooperation and selection occur within the same species in intraspecific cooperation. Based on the analysis of Killingback and Doebeli (2002) we show analytically that this difference indeed implies that neither the small initial offer nor the reward rate can increase by variable investment, except at very special and biologically irrelevant combinations of parameters. Evolution of mutualism is thus essentiallyimpossible in spatially non-structured version of the Doebeli and Knowlton's (1998) model.

We are interested in whether the initially small and positive parameters α_i and β_i $(i = h, s)$ can increase in the iterated investment game model of mutualism. For small values of these parameters the investment I determined by Eqs. (1), (2) are also small. Therefore it is enough to consider the linear approximations of $C(I)$ and $B(I)$, that is $C(I) = C_0 I$ and $B(I) = B_0 I$, where $C_0 = C'(0)$ and $B_0 = B'(0)$ are the derivatives of the functions at $I = 0$ (Killingback and Doebeli, 2002).

Let us assume that a small ε fraction of individuals mutate to α'_i, β'_i phenotypes in both species. Using Eqs. (1), (2) and the linear approximations of the cost and benefit functions, we obtain a recursive equation for the payoffs of resident and mutant phenotypes for both species

$$\begin{aligned}
S_h^{(k+1)} &= B_0[(1-\varepsilon_h)(\alpha_s + \beta_s S_s^{(k)}) + \varepsilon_h(\alpha'_s + \beta'_s {S'_s}^{(k)})] \\
&\quad - C_0(\alpha_h + \beta_h S_h^{(k)}), \\
{S'_h}^{(k+1)} &= B_0[(1-\varepsilon_h)(\alpha_s + \beta_s S_s^{(k)}) + \varepsilon_h(\alpha'_s + \beta'_s {S'_s}^{(k)})] \\
&\quad - C_0(\alpha'_h + \beta'_h {S'_h}^{(k)}), \\
S_s^{(k+1)} &= B_0[(1-\varepsilon_s)(\alpha_h + \beta_h S_h^{(k)}) + \varepsilon_s(\alpha'_h + \beta'_h {S'_h}^{(k)})] \\
&\quad - C_0(\alpha_s + \beta_s S_s^{(k)}), \\
{S'_s}^{(k+1)} &= B_0[(1-\varepsilon_s)(\alpha_h + \beta_h S_h^{(k)}) + \varepsilon_s(\alpha'_h + \beta'_h {S'_h}^{(k)})] \\
&\quad - C_0(\alpha'_s + \beta'_s {S'_s}^{(k)}). \qquad (3)
\end{aligned}$$

Here we assumed that an (α_i, β_i) strategy obtains an average benefit from its mutualistic partner proportional to the frequency of the strategies present in that population, that is, there is a "playing the field" situation in well-mixed populations (Maynard Smith, 1982). Killingback and Doebeli (2002) restricted their attention to the infinitely large population limit ($\varepsilon_i = 0$), thus their model is generalized here to the case $\varepsilon_h, \varepsilon_s \neq 0$. If there are high numbers of interactions between two generations ($k \gg 1$), then $S_i^{(k)}$ and ${S'_i}^{(k)}$ can be considered as the S_i, S'_i fixed points of Eqs. (3). Thus, the fitness of a strategy (α_i, β_i) is approximately kS_i. Since the fitnesses of both the resident and the mutant strategies are multiplied with the same constant k, it is enough to consider the S_i, S'_i fixed points in the following (Killingback and Doebeli, 2002). The fixed points can be computed from the linear recursion system (3), but they are too complex to display here (but see Appendix A). The relevant points here are that the fixed points exist, and they are asymptotically stable if β_i and β'_i are sufficiently small (Appendix B). To make the stability analysis tractable we assume here and in the following that $\varepsilon_h = \varepsilon_s = \varepsilon$.

Since the initial offer (α_i) and reward rate (β_i) are continuous variables, it is convenient to use adaptive dynamics to investigate the evolution of mutualism (Hofbauer and Sigmund, 1990; Geritz et al., 1998; Metz et al., 1992; Killingback and Doebeli, 2002). According to this framework, the dynamics of phenotypic traits are

$$\dot{\alpha}_i = \left.\frac{\partial S_i'}{\partial \alpha_i'}\right|_{(\alpha_i'=\alpha_i,\beta_i'=\beta_i)},$$

$$\dot{\beta}_i = \left.\frac{\partial S_i'}{\partial \beta_i'}\right|_{(\alpha_i'=\alpha_i,\beta_i'=\beta_i)}, \tag{4}$$

where i denotes either the host (h) or the symbiont (s) species. Since our analysis is restricted to the invasion of rare mutants we can assume that $\varepsilon \ll 1$, thus we can consider the linear approximation of S_i' in ε (see Appendix A). Thus we obtain a relatively simple form from Eq. (4)

$$\dot{\alpha}_i = \frac{1}{1 + C_0\beta_i}\left(-C_0 + \frac{B_0^2\beta_j}{\Gamma}\varepsilon\right),$$

$$\dot{\beta}_i = \frac{\Lambda_i}{(1 + C_0\beta_i)\Gamma}\left(-C_0 + \frac{B_0^2\beta_j}{\Gamma}\varepsilon\right), \tag{5}$$

where $\Gamma = 1 + C_0(\beta_s + \beta_h) + (C_0^2 - B_0^2)\beta_s\beta_h$, $\Lambda_i = \alpha_i[-C_0 + (B_0^2 - C_0^2)\beta_j] + B_0\alpha_j$, and i, j indexes denote h or s respectively. Mutualism emerges if the originally small α_i and β_i increase, that is if the right-hand sides of (5) are positive (Killingback and Doebeli, 2002).

It can be seen from Eqs. (5) that the originally small α_i decreases further at the infinite population size limit ($\varepsilon = 0$). The parameters β_i can increase when Λ_i/Γ is negative. Since β_i is small for both partners, Γ can be considered a positive number in this limit. However, if $\beta_i < \frac{C_0}{B_0^2 - C_0^2} = \beta_c$ and α_i is sufficiently smaller than α_j then Λ_i can be negative. In this case β_i increases, until it reaches a limit which is definitely smaller than β_c. Consequently, the initial offer (α_i) decreases, the reward rates (β_i) either increases or decreases initially, but cannot exceed the β_c, thus there is no way for evolution of mutualism in the infinite population size limit.

Now let us analyse the case when the population is finite and mutants are rare ($0 < \varepsilon \ll 1$). Remember that β could not be arbitrarily close to zero to increase even in the single species cooperative model, so it is possible that reasonable small thresholds exist here as well, above which α_i and β_i will increase. Observe, that if Γ remains positive, but it is close to zero then the expressions in the parentheses of Eqs. (5) can be positive. Since we focus on the emergence of mutualistic interactions from a non-mutualistic state we assume that α_i and β_i are close to zero initially. Further, we assume that the initial propensity to the mutualistic interaction are roughly the same for both species ($\alpha_h \approx \alpha_s$ and $\beta_h \approx \beta_s$) and for the phenotypic traits ($\alpha_i \approx \beta_i$) too. Naturally, this is not sufficiently the case, but without these assumptions the analysis become hopelessly complex. To make the estimation more tractable, let us assume in the future that initially $\alpha_i = \beta_i = \beta$. The expressions in the parentheses of Eqs. (5) can be positive if $0 < \Gamma \ll 1$ which relations are valid if β is close to but still smaller than $\beta_{tr} = 1/(B_0 - C_0)$. (If $\beta > 1/(B_0 - C_0)$ then $\Gamma < 0$, and thus α_i will decrease if Γ is a large positive number then the second term can be neglected in the parentheses of Eqs. (5), and this α_i will decrease again). To satisfy this condition we assume that$\beta = (1 - \delta)\beta_{tr}$, where $0 < \delta < 1$ measures the deviation from the threshold β_{tr}. Using this notation and assuming that $\delta^2 \ll \delta$ we conclude that $\Gamma \approx \frac{2\delta B_0}{B_0 - C_0}$ in the δ neighborhood of β_{tr}. Substituting these values of β and Γ into the first equation of Eqs. (5) and rearranging the expression in the parentheses, we conclude that α_i increases if

$$\delta < \frac{B_0\varepsilon}{B_0\varepsilon + 2C_0} = \delta_{tr}. \tag{6}$$

The same condition for δ guarantees that the expression in the parentheses in the second equation of Eqs. (5) is positive as well, but $\dot{\beta}_i$ will be positive only if $\Lambda_i > 0$ at the same time. Substituting $(1 - \delta)\beta_{tr}$ for β yields $\Lambda_i = 1 - \delta + \frac{B_0 + C_0}{B_0 - C_0}(1 - 2\delta)$, which is positive, at least if δ is not too close to one. We thus conclude that the parameters α_i and β_i will increase if

$$(1 - \delta)\beta_{tr} < \beta < \beta_{tr}. \tag{7}$$

The evolution of mutualism is possible if both β_{tr} and δ_{tr} are not very close to zero. In this case, the initially small α_i, β_i trait values will increase in a relatively wide interval of α and β (see Eqs. (6) and (7)). The parameter β_{tr} is not too small if B_0 is not much higher than C_0. However, since ε is a small number, thus δ_{tr} is close to zero in this case. That is, α_i and β_i can increase only in a restricted interval of β around a relatively high value (see Eq. (7)). According to Eq. (6) the parameter δ_{tr} can be relatively large if $B_0 \gg C_0$, but then $\beta_{tr} \ll 1$. Consequently, this analysis confirms the numerical results of Doebeli and Knowlton (Doebeli and Knowlton, 1998): that it is highly improbable that mutualistic interaction would emerge in this model system. We emphasize here that our analysis is restricted only to the large population limit ($\varepsilon \ll 1$), which could not exclude the evolution of mutualism in small populations. Similarly, our conclusion does not exclude the possibility of the emergence of mutualism in cases when the initial α_i and β_i values differ to each other meaningfully (e.g. $\alpha_h/\alpha_s \ll 1$, $\beta_h/\beta_s \ll 1$, etc.), although these conditions seems to be biologically less relevant. On the other side, this Letter emphasizes indirectly the important role of spatial structures in the evolution of mutualism.

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Appendix A. The fixed point

The fixed points of Eq. (3) are

$$S_i = \frac{1}{1 + C_0\beta_i}\frac{C_0(\alpha_i - \alpha'_i) + \Phi_i}{\Theta_i},$$

$$S'_i = \frac{B_0^2 C_0(1-\varepsilon)(\alpha'_i - \alpha_i)\beta_i[\varepsilon(\beta_j - \beta'_j) - \beta_j(1 + C_0\beta'_j)] + \Phi_i}{\Theta_i}, \tag{A.1}$$

where i denotes either the host or the symbiont. Φ_i and Θ_i are

$\Phi_i = B_0^2\beta_i C_0(1-\varepsilon)(\alpha'_i - \alpha_i)[\varepsilon(\beta_j - \beta'_j) - \beta_j - C_0\beta_j\beta'_j] + (1 + C_0\beta'_j)\beta_j B_0(\varepsilon - 1) \quad [C_0\alpha_j - B_0\alpha_i((1-\varepsilon) + \varepsilon\alpha'_i] + (1 + C_0\beta_i)[B_0\alpha_j(\varepsilon - 1) - B\varepsilon\alpha'_j + C_0\alpha'_i)](1 + C_0\beta'_j)$,

$\Theta_i = (1 + C_0\beta'_i)\beta_i B_0^2(1-\varepsilon)[\varepsilon\beta'_j + \beta_j(1-\varepsilon) + C_0\beta'_j] + (1 + C_0\beta_i)[B_0^2(1-\varepsilon)\varepsilon\beta_j\beta'_i \qquad (1 + C_0\beta'_j) + (1 + C_0\beta_j)(B_0^2\varepsilon^2\beta'_j\beta'_i - (1 + C_0\beta'_j)(1 + C_0\beta'_i))]$, where the i,j indexes denote different species.

To determine the adaptive dynamics of α_i and β_i we have to differentiate the fixed points within respect to these variables. This operation yields another complex expression, which can be simplified by using that $\varepsilon \ll 1$. Considering the linear approximation of the derivatives in the function of ε we arrive at Eq. (4). The calculations have been performed by the software Mathematica 3.0.

Appendix B. The stability of the fixed point

The analysis of the stability of the fixed points in the two-species case is not as simple as in the one species case (Killingback and Doebeli, 2002), but is still tractable. $\mathbf{A}_\varepsilon$, the Jacobian matrix of (3) can be considered as $\mathbf{A} + \varepsilon\mathbf{B}$, where

$$\mathbf{A} = \begin{pmatrix} -C_0\beta_h & 0 & B_0\beta_s & 0 \\ 0 & -C_0\beta'_h & B_0\beta_s & 0 \\ B_0\beta_h & 0 & -C_0\beta_s & 0 \\ B_0\beta_h & 0 & 0 & -C_0\beta'_s \end{pmatrix},$$

$$\mathbf{B} = \begin{pmatrix} 0 & 0 & -B_0\beta_s & B_0\beta'_s \\ 0 & 0 & -B_0\beta_s & B_0\beta'_s \\ -B_0\beta_h & B_0\beta'_h & 0 & 0 \\ -B_0\beta_h & B_0\beta'_h & 0 & 0 \end{pmatrix}.$$

To determine the eigenvalues of the Jacobian matrix is a hopeless task, but since $\varepsilon \ll 1$ it can be considered as a perturbation of matrix $\mathbf{A}$. The eigenvalues of $\mathbf{A}$ are $-C_0\beta'_h, \frac{1}{2}(-C_0(\beta_h + \beta_s) - \sqrt{4(B_0^2 - C_0^2) + C_0^2(\beta_h + \beta_s)^2}),$ $\frac{1}{2}(-C_0(\beta_h + \beta_s) + \sqrt{4(B_0^2 - C_0^2) + C_0^2(\beta_h + \beta_s)^2}), -C_0\beta'_s$. It is known that if $\mathbf{A}_\varepsilon = \mathbf{A} + \varepsilon\mathbf{B}$ where ε is a small number then $|\lambda_i(\mathbf{A}) - \lambda_i(\mathbf{A}_\varepsilon)| \leqslant cond(\mathbf{S})\|\mathbf{B}\|\varepsilon$ (Kato, 1980). The matrix $\mathbf{S}$ diagonalizes $\mathbf{A}$, that is $\mathbf{S}^{-1}\mathbf{A}\mathbf{S} = diag(\lambda_i(\mathbf{A}))$. $cond(\mathbf{S}) = \|\mathbf{S}^{-1}\|\|\mathbf{S}\|$ is the condition number of $\mathbf{S}$. Since the eigenvectors of $\mathbf{A}$ are not closely parallel, the condition number of $\mathbf{S}$ cannot be high, and therefore the estimation is not ill-conditioned (Demmel, 1997). Using the euclidean norm for $\mathbf{B}$ it can be shown that

$$|\lambda_i(\mathbf{A}) - \lambda_i(\mathbf{A}_\varepsilon)| \leqslant cond(\mathbf{S})\sqrt{2}B_0 \max\left\{\sqrt{\beta_h^2 + \beta'^2_h}, \sqrt{\beta_s^2 + \beta'^2_s}\right\}\varepsilon. \tag{B.1}$$

Thus the condition of $|\lambda_i(\mathbf{A})| < 1$ gives a good estimation for $|\lambda_i(\mathbf{A}_\varepsilon)|$ to be smaller than one, which guarantees the stability of the fixed points. It follows from simple calculations that $|\lambda_i(\mathbf{A})| < 1$ is valid if $\beta'_h < 1/C_0$, $\beta'_S < 1/C_0$, and $2 > 1 + \beta_h\beta_s(C_0^2 - B_0^2) > (\beta_h + \beta_s)C_0$, which is true if β_i and β'_i are small enough.

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